Journal of Applied Ecology

British Ecological Society

Journal of Applied Ecology 2011, **48**, 133–142 doi: 10.1111/j.1365-2664.2010.01897.x

Cost-effective age structure and geographical distribution of boreal forest reserves

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Summary

1. Forest reserves are established to preserve biodiversity, and to maintain natural functions and processes. Today there is heightened focus on old-growth stages, with less attention given to early successional stages. The biodiversity potential of younger forests has been overlooked, and the cost-effectiveness of incorporating different age classes in reserve networks has not yet been studied.

2. We performed a reserve selection analysis in boreal Sweden using the Swedish National Forest Inventory plots. Seventeen structural variables were used as biodiversity indicators, and the cost of protecting each plot as a reserve was assessed using the Heureka system. A goal programming approach was applied, which allowed inclusion of several objectives and avoided a situation in which common indicators affected the result more than rare ones. The model was limited either by budget or area.

3. All biodiversity indicators were found in all age classes, with more than half having the highest values in ages ≥ 100 years. Several large-tree indicators and all deadwood indicators had higher values in forests 0–14 years than in forests 15–69 years.

4. It was most cost-effective to protect a large proportion of young forests since they generally have a lower net present value compared to older forests, but still contain structures of importance for biodiversity. However, it was more area-effective to protect a large proportion of old forests since they have a higher biodiversity potential per area.

5. The geographical distribution of reserves selected with the budget-constrained model was strongly biassed towards the north-western section of boreal Sweden, with a large proportion of young forest, whereas the area-constrained model focussed on the south-eastern section, with dominance by the oldest age class.

6. *Synthesis and applications*. We show that young forests with large amounts of structures important to biodiversity such as dead wood and remnant trees are cheap and cost-efficient to protect. This suggests that reserve networks should incorporate sites with high habitat quality of different forest ages. Since young forests are generally neglected in conservation, our approach is of interest also to other forest biomes where biodiversity is adapted to disturbance regimes resulting in open, early successional stages.

Key-words: biodiversity, conservation planning, early succession, goal programming, indicator, old-growth, reserve selection, Swedish National Forest Inventory, young forest

Introduction

The boreal forest belt runs circumpolar in the Northern Hemisphere and comprises more than 30% of all global forest area, with Russia and Canada having by far the largest area covered in forest (FAO 2006). Although northern Europe has a comparatively small forested area, forests are the dominant

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ecosystem type, and the forest industry is a major export industry in several northern European countries. For example, intensive forestry has been conducted since the mid 20th century in Sweden on a large proportion of the productive forest land, and this has led to even-aged and fragmented forest landscapes with small amounts of important features for biodiversity such as dead wood and old trees (Östlund, Zackrisson & Axelsson 1997; Löfman & Kouki 2001). In the past boreal forests were mainly shaped by fire (Zackrisson 1977), leading to a dynamic forest structure consisting of stands with different ages (Angelstam 1998). As a consequence of fire exclusion and suppression, today few natural forests remain and hundreds of species are threatened (Esseen *et al.* 1997; Gärdenfors 2005). To mitigate this situation, reserves have been established with the aim of maintaining natural functions and processes, and preserving indigenous species in viable populations (Swedish Government 2005). Today, 1% of the productive boreal forests in Sweden below the mountain region are protected in reserves or in national parks (Anonymous 2007a).

To rationalize the process of finding and designing reserves, a systematic approach to conservation planning has been developed in which complementarity and representativeness are key aspects (Margules & Pressey 2000). One way for forests in a reserve network to represent a natural range of structures and composition is to include different successional stages (Junninen *et al.* 2006). This composition approach has been largely overlooked in forest conservation strategies. For instance, in boreal Sweden, 76% of the protected forests are over 100 years and only 1·5% are under 15 years (NFI data). Since humans have affected the forests in boreal Fennoscandia for centuries, knowledge of the natural age composition in the forest landscape is lacking. Most probably, the amount of open areas and remnant structures varied substantially in space and time depending on disturbance pattern, indicating a complex forest composition (Kuuluvainen 2009).

A post-disturbance deciduous forest with large amounts of dead wood is one of the most species-rich forest types in the boreal zone because of the possibility of existence for species adapted to both early and late successional stages (Esseen *et al.* 1997). Young natural forests have a unique species composition not found in any other successional stage (Spies & Franklin 1991; Swanson *et al.* 2010) and early successional stages are considered important for the protection of some red-listed species (Tikkanen *et al.* 2006). Many of the species associated with old-growth forests might not be dependent on old forests *per se*, but more on structures occurring there, e.g. dead wood (Kouki *et al.* 2001).

To our knowledge, research has not been conducted on the value of including forests of different ages in boreal forest reserve networks. The annual National Forest Inventory (NFI) in Sweden offers an opportunity for such studies because of the large number of plots surveyed and the data collected on a number of structural variables such as dead wood, tree species, tree sizes and ages (Ranneby *et al.* 1987). Since the economic value of forests varies greatly with forest age, economic aspects are also important to consider, and can be calculated with high precision for the NFI plots.

The main aim of our study was to analyse the cost-effectiveness and biodiversity potential of protecting forests in different age classes. To investigate this, optimal combinations of forest age classes with different constraints regarding area and budget were identified. A reserve selection framework building on optimization models was applied with the potential for biodiversity assessed from structural forest characteristics. In addition, geographical differences in the distribution of reserves were studied using models constrained by area and budget.

Materials and methods

STUDY AREA AND NFI

The study area covered the counties of Värmland, Örebro, Dalarna, Gävleborg, Jämtland, Västernorrland, Västerbotten and Norrbotten (about 14 million ha of productive forest land), an area roughly coinciding with the boreal zone in Sweden (Ahti, Hämet-Ahti & Jalas 1968). The boreal forest is characterized by a relatively homogeneous structure dominated by Scots pine *Pinus sylvestris* L. and Norway spruce *Picea abies* (L.) Karst. The main broad-leaved trees are birches *Betula pendula* Roth. and *B. pubescens* Ehrh. and aspen *Populus tremula* L. (Gustafsson & Ahlén 1996).

NFI is an annual survey of all land in Sweden that started in 1923 (Anonymous 1932), with a present systematic cluster design that was established in 1983 (Ranneby *et al.* 1987). Circular sample plots with a diameter of 7 or 10 m are clustered along the borders of square tracts, with a total of approximately 11 000 plots surveyed each year (Anonymous 2007b). Two-thirds of the tracts are permanent and are surveyed every fifth year, whereas the remaining one-third of the tracts are surveyed only once. Plot numbers and tract sizes differ between regions and between permanent and temporary tracts (Anonymous 2005).

In this study, temporary and permanent NFI-plots within the study area were used from productive forest land outside of reserves and surveyed between the years 2003 and 2007 (17 599 plots in total). For the analysis, the plots were aggregated into 112 larger 50×50 km plots; 292 NFI-plots were excluded since a 50×50 km plot had to contain a minimum of 30 NFI-plots. The excluded plots were located along the outer border of the study area. The 50×50 km plots were in turn grouped into 6 geographical regions (Fig. 1) matching administrative county borders. Four smaller counties were grouped together (two and two) in order to make the regions more equally sized. The forest within each aggregated 50×50 km plot was divided into five age classes: 0–14, 15–39, 40–69, 70–99 and ≥ 100 years, with the total area in each age class comprising 2·3, 3·4, 2·9, 2·0 and 3·6 million ha respectively. Age class division was based on the introduction of tree retention practices (Lindenmayer & Franklin 2003) about 15 years ago, and on a normal rotation time of about 100 years.

BIODIVERSITY INDICATORS

Structure-based indicators registered in the NFI were used as proxies for biodiversity potential. We chose indicators based on what are commonly thought to be the important substrates and environmental conditions for a majority of forest species (Ferris & Humphrey 1999; Lindenmayer, Margules & Botkin 2000; Spanos & Feest 2007): structural heterogeneity in the form of gaps and water dynamics (Kuuluvainen 2002); uneven age and multi-layered tree canopy (Esseen *et al.* 1997); deciduous trees (both old trees in conifer forests and younger ones in early successional deciduous forests) (Hagar

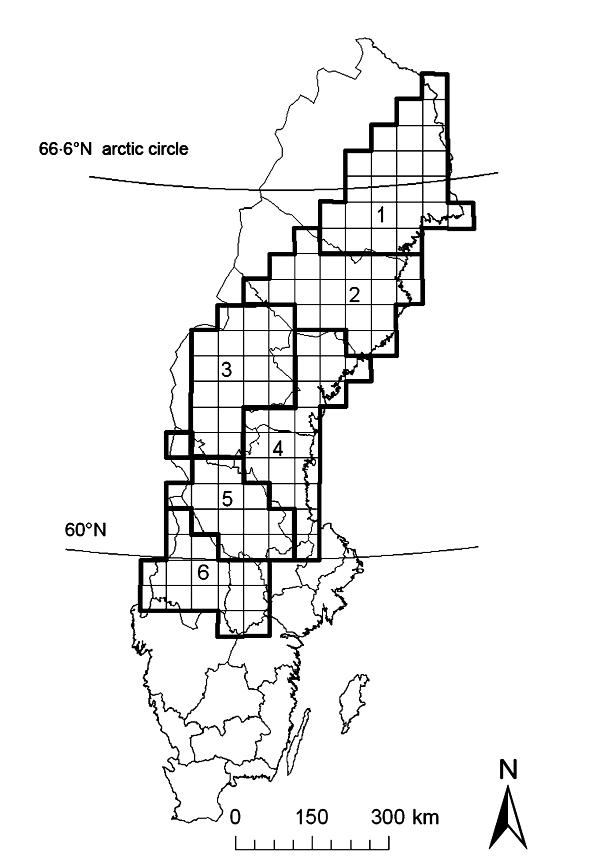

Fig. 1. Map of the study area. The analysed NFI-plots were grouped into 50 × 50 km large plots which were further aggregated into 6 geographical regions, broadly following the borders of administrative counties: 1. Norrbotten, 2. Västerbotten, 3. Jämtland, 4. Västernorrland and Gävleborg, 5. Dalarna, 6. Värmland and Örebro.

2007); and large-diameter trees and dead wood (Nilsson, Hedin & Niklasson 2001; Siitonen 2001). The underlying assumption was that the potential for high richness of indigenous species, including rare species, would increase if the presence of structural indicators was maximized. Forests with large trees, plentiful dead wood and dying trees, and a high proportion of broad-leaved trees should currently be prioritized in forest conservation according to political guidelines (Swedish Government. 2005).

The registration of each indicator on the NFI plots was translated into a point between 0 and 100 (Table 1), and each aggregated 50 × 50 km plot was given a biodiversity indicator point ha^{-1} for each indicator and age class. The biodiversity indicator point ha^{-1} was calculated as the sum of points (for each indicator) from all NFI plots in the 50 × 50 km plot (in each age class) divided by the total area that all NFI plots in the 50 × 50 km plot (in each age class) represent. The indicator 'volume of dead wood' was calculated as the total volume of dead wood (for each age class) in the 50 × 50 km plot divided by the total area (for each age class). This point was normalized from 0 to 100 for all volumes less than or equal to 20 m^3 ha^{-1}. Volumes greater than 20 m^3 ha^{-1} were given 100 points to avoid disproportional influence of outliers. The presence of the exotic *Pinus contorta* Dougl. var. *latifolia* Engelm and the stand character 'plantation character' (no structures from previous stands, > 90% of the trees of the same species, even-aged and consisting of one layer) were considered negative for biodiversity, and plots with these registrations were excluded from the selection (1005 plots) since it would not be realistic to establish a reserve in an area containing a plantation.

OPPORTUNITY COST

The opportunity cost, i.e. the economic value of the plots, was estimated by using the net present value (NPV) from future forestry activities. The NPV was based on the sum of income and cost of future activities from timber harvest from period one to infinity discounted back to today with a 3% interest rate. This is consistent with the value of an investment of moderate risk in northern Europe (Ibbotson & Sinquefield 1986). For each plot, up to 100 different treatment schedules were first simulated using the Heureka system and then the most profitable schedule was selected to calculate the economic value. The Heureka system is a newly developed planning system for multiple-use forestry (Lämås *et al.* 2006). Each treatment schedule consisted of variable timing for the associated silvicultural activities from period one to infinity (i.e. thinning and clear cutting with appropriate regeneration following a harvest). Economic data (timber, regeneration and harvesting costs) used for calculating the NPV for each schedule were based on a timber price list for 2008 retrieved from the forest owners' association in northern Sweden, and was representative for the region.

DECISION MODELS

There were large differences in points between indicators; therefore a method that could accommodate these variations was essential. When using ordinary linear programming (LP) it is necessary to find weights for each indicator to include into one single objective function. We used a goal programming approach to allow impartial treatment of all indicators and avoid manual weight determination. In a two-phase approach, we first found the best possible outcome for each indicator, which became a goal. In the second phase, we searched for a solution that was as close as possible to each individual indicator goal but that considered all indicators at the same time. Each of the models used are described below (see Table 2 for parameters and decision variables).

The first LP problem can be formulated as follows:

$$[\mathrm{P1}]\max z = \sum_{i\in I}\sum_{t\in T}\sum_{e\in E} w_e p_{ite} x_{it} \qquad \text{eqn 1}$$

subject to

$$\sum_{i\in I}\sum_{t\in T} c_{it}x_{it} \le b \qquad \text{eqn 2}$$

$$\sum_{i\in I}\sum_{t\in T} x_{it} \le q\sum_{i\in I}\sum_{t\in T} a_{it} \qquad \text{eqn 3}$$

$$x_{it} \le a_{it}, \forall i \in I, t \in T \qquad \text{eqn 4}$$

$$x_{it} \ge 0, \forall i \in I, t \in T \qquad \text{eqn 5}$$

The objective function, eqn 1, maximizes the sum of the points from the biodiversity indicators in the selected areas (hereafter referred to as the biodiversity indicator score). Constraint set in eqn 2 is the budget constraint preventing the total cost of the selected areas to exceed the available budget (b). Constraint set in eqn 3 is the area constraint, preventing the total selected area from exceeding a certain proportion (q) of the total area. Constraint set in eqn 4 ensures that the area selected from each 50 × 50 km plot and age class is smaller than its existing area, and set in eqn 5 is the non-negativity constraints on the decision variables.

Table 1. List of biodiversity indicators and criteria for points

Indicator	100 points	50 points	0 points
Uneven age[1]	Not even-aged	Fairly even-aged	Completely even-aged
Gaps[2]	Several gaps	Some gaps	No gaps
Stand character[3]	Pristine		Normal
Tree layer[4]	Fully layered/several layers	Two layers	One layer/no layer
Ground structure[5]	Very uneven/fairly uneven	Fairly even	Very even
Large pine	>40 cm dbh	>30 cm dbh	Not present
Large spruce	>40 cm dbh	>30 cm dbh	Not present
Large birch	>40 cm dbh	>30 cm dbh	Not present
Large aspen	>40 cm dbh	>30 cm dbh	Not present
Large deciduous tree (other than aspen or birch)	>40 cm dbh	>30 cm dbh	Not present
Dead conifer tree lying	Tree $>$ 20 cm dbh		Not present
Dead deciduous tree lying	Tree $>$ 20 cm dbh		Not present
Dead conifer tree standing	Tree $>$ 20 cm dbh		Not present
Dead deciduous tree standing	Tree $>$ 20 cm dbh		Not present
Presence of rowan	Present		Not present
Affected by water (moving water/spring/temporarily flooded)	Yes		No
Volume of dead wood	>20 m^3 ha^{-1}	≤ 20 m^3 ha^{-1}*	

*Normalized point according to the volume of dead wood ha^{-1}, from 0 to 100.
[1]Totally even-aged: $>$ 95% of the volume within an age interval of 5 years, fairly even-aged: $>$ 80% of the volume within an age interval of 20 years; remaining stands classed as uneven aged.
[2]Gap: an area without main crop seedlings/main trees larger than a square with a length of 2·5 times the average distance between main crop seedlings/main trees, but at least 5 m. Several gaps: at least 4 gaps within a 20 m radius from the centre of the plot, some gaps: 2–3 gaps; remaining stands are classed as no gaps.
[3]Pristine character: presence of coarse ($>$ 25 cm diameter) dead wood and no trace of management actions during the last 25 years.
[4]Tree layer: group of trees amongst which the height is approximately the same, but their mean height differs from other layers. Fully layered: all diameter classes represented, the biggest tree $>$ 20 cm in diameter, the number of stems increasing with increasing diameter class, and the volume density (relationship between the actual volume in the stand and the potential volume) $>$ 0·5.
[5]Ground structure: Classification based on height and frequency of irregularities (rocks, small hills and holes) on the ground.

Table 2. Parameters and decision variables for the model

Notation	Description
Parameters	
I	Set of 50 × 50 km plots (i = 1,...,n)
T	Set of age classes (t = 1,...,m)
E	Set of biodiversity indicators (e = 1,...,o)
p_{ite}	Point of biodiversity indicator e in plot i and age class t
a_{it}	Area (ha) of plot i in age class t
c_{it}	Cost ha^{-1} of plot i and age class t
w_e	Weight of biodiversity indicator e
q	Maximum proportion that can be selected
b	Available budget (SEK)
Decision variables	
x_{it}	Area (ha) selected in plot i and age class t

It is difficult to establish weights w_e that can be considered to be appropriate (Polasky, Camm & Garber-Yonts 2001). Typically, an indicator with large value will dominate and the solution tends to select areas with high values for one (or maybe a few) indicators. Goal programming is an approach that includes several objectives (expressed as goals) in the same objective function and still allows a trade-off that is considered impartial. In goal programming, we establish goals in phase 1. In our case, we simply solved the problem [P1] as many times as we had different indicators. When we solved [P1] for indicator e, we set w_e to 1 for that indicator and 0 for all other indicator weights. This means that we independently searched for the best possible value for each indicator. We let those 17 values be denoted as z_e.

In the second phase, we wanted to find a solution in which all indicators were as close as possible to their goal. Since it would not be possible to reach the goal of each indicator, a quadratic deviation from these goals was minimized. The goal programming model in phase 2 can be formulated as

$$[\text{P2}]\ \min w = \sum_{e\in E}\left(\left(z_e - \sum_{i\in I}\sum_{t\in T} p_{ite}x_{it}\right)/z_e\right)^2 \qquad \text{eqn 1b}$$

subject to
eqns 2–5

In this objective function, eqn 1b, the squared difference between the goal and the actual biodiversity indicator score for each indicator is minimized. The difference is scaled with the goal value and hence we measure the deviation as a percentage deviation. Problem [P2] is a quadratic programming problem. The problem is convex (Lundgren, Rönnqvist & Värbrand 2010) so a global optimal solution is guaranteed.

The models were formulated in the modelling language AMPL and solved using the software CPLEX 11·2 (ILOG 2006). All tests were conducted on a standard PC with 2·99 GHz and 3·25 GB of internal memory. The number of variables (in both models) was 9520 (112*5*17) and the number of constraints was 562 (1 + 1 + 112*5). The solution time for each problem was within a fraction of a second.

Results

BIODIVERSITY INDICATORS

In the original NFI data used for analysis, the biodiversity indicators were distributed unevenly over the five age classes, but with all indicators represented in all age classes (Table 3). The

Table 3. Biodiversity indicator data from NFI (based on individual plots) with mean points ± standard deviation, as well as total area and total cost for the five age classes

	Age class				
	0–14	15–39	40–69	70–99	≥ 100
Biodiversity indicator					
Uneven age	7·8 ± 18·8	28·4 ± 27·4	45·1 ± 28·0	63·3 ± 27·0	73·8 ± 27·2
Gaps	15·7 ± 31·6	21·3 ± 34·0	27·7 ± 37·0	24·8 ± 35·1	29·0 ± 36·7
Stand character	0·03 ± 1·8	0·13 ± 3·6	0·14 ± 3·8	0·61 ± 7·8	3·65 ± 18·8
Tree layer	24·5 ± 30·5	42·5 ± 27·3	43·6 ± 29·8	48·1 ± 30·6	45·3 ± 30·8
Ground structure	35·3 ± 40·4	36·6 ± 41·0	31·4 ± 39·4	29·1 ± 39·4	35·3 ± 41·9
Large pine	5·8 ± 19·5	1·4 ± 10·1	6·7 ± 19·8	15·5 ± 27·9	22·5 ± 31·1
Large spruce	0·2 ± 2·9	0·6 ± 5·7	5·5 ± 18·0	13·3 ± 27·0	13·9 ± 27·8
Large birch	0·4 ± 5·4	0·2 ± 3·3	1·7 ± 9·9	1·9 ± 10·1	0·9 ± 7·2
Large aspen	0·3 ± 4·6	0·2 ± 3·6	0·6 ± 6·1	0·7 ± 6·8	0·6 ± 6·4
Large deciduous tree (other than aspen or birch)	0·1 ± 2·3	0·2 ± 3·9	0·4 ± 5·1	0·3 ± 4·6	0·3 ± 4·6
Dead conifer tree lying	13·2 ± 33·8	7·3 ± 25·9	6·2 ± 24·1	10·5 ± 30·6	15·8 ± 36·5
Dead deciduous tree lying	3·6 ± 18·5	1·5 ± 12·3	1·7 ± 12·8	2·2 ± 14·5	2·5 ± 15·7
Dead conifer tree standing	4·9 ± 21·6	1·1 ± 10·5	2·4 ± 15·4	7·5 ± 26·3	12·0 ± 32·5
Dead deciduous tree standing	1·0 ± 9·7	0·3 ± 5·3	0·8 ± 8·9	2·4 ± 15·2	2·4 ± 15·3
Presence of rowan	34·4 ± 47·5	32·0 ± 46·7	29·1 ± 45·4	21·7 ± 41·3	15·3 ± 36·0
Affected by water (moving water/spring/temporarily flooded)	0·8 ± 9·0	1·1 ± 10·4	1·9 ± 13·7	1·6 ± 12·5	1·9 ± 13·6
Volume of dead wood	23·2 ± 34·1	10·3 ± 23·1	17·1 ± 29·3	29·6 ± 37·5	37·1 ± 40·1
Total area (1000 ha)	2346	3396	2975	2021	3550
Total cost (billion SEK)	21·6	67·8	87·8	74·7	141·6

The points for the indicator 'Volume dead wood' were given proportionally to the volume ha^{-1}, with volumes > 20 m^3 ha^{-1} given 100 points. The actual volumes per 1000 ha are shown.

relative magnitude of the mean points should not be interpreted as a sign of importance since the optimization models neutralized the advantage of common indicators. Instead differences between age classes are of interest. More than half of the 17 indicators peaked at ages > 100 years. Several of the large-tree indicators and all deadwood indicators had a higher mean point in the youngest forests (0–14 years) than in the subsequent age class. All deadwood indicators had the lowest values at intermediate age classes. 'Uneven age' increased over time, whereas 'rowan' decreased.

OPTIMAL AGE DISTRIBUTIONS

To investigate the question of whether the optimal combination of forest ages differed when a budget constraint or an area constraint were used, two versions of the stated model were solved. In the first version, budget was limiting (i.e. the area constraint, eqn 3, was omitted). This model was solved 100 times with an incremental increase in budget, starting at 1% of the total cost of all forest, up to 100%, with automatic registration of age distribution in each stage, resulting in 1800 ((17 + 1)*100) optimizations. In the second version, area was limiting and the budget constraint, eqn 2, was omitted. This model was also solved 100 times, with an incremental increase in area limit, starting at 1% of the total area, up to 100%, also with automatic registration of age distribution in each stage.

The optimal age distributions when cost was limiting differed markedly from the optimal age distributions when area was limiting. With a budget-constrained approach, a large proportion of young forest was chosen at small budgets (Fig. 2a) whereas forests in the 40- to 99-year age class were selected to a lower extent. However, when the selection was made with an area-constrained approach, the proportion of old forest was clearly more dominant (Fig. 2b). Forests in the 15- to 39-year age class were selected the least when costs were not considered, but younger forests were also selected in small proportions at low area limits. In general, the area-constrained approach covered less area but with higher biodiversity indicator scores, whereas the budget-constrained approach covered more area, but with lower biodiversity indicator scores (Fig. 3). The budget-constrained approach achieved a higher biodiversity indicator score compared to the area-constrained approach at any given cost (Fig. 3a).

GEOGRAPHICAL DISTRIBUTION

Two scenarios were used to analyse the differences in geographical distribution of selected forests between a budget-constrained model and an area-constrained model. In the first scenario, a budget was set to 10 billion SEK (2·5% of the cost for the total area). The limit was chosen based on the current political targets in Sweden for nature reserve establishment, with 6 billion SEK allocated to forest protection for the years 1998–2008 (Swedish Government 2009). The area limit was set to 714 000 ha (5% of the total area) since this scenario gave approximately the same biodiversity indicator score.

The 10 billion SEK budget scenario led to a reserve area of 1·2 million ha with a strong bias for selection of areas in the north-western section of boreal Sweden (Fig. 4a). The scenario with an area limit of 714 000 ha corresponded to a cost

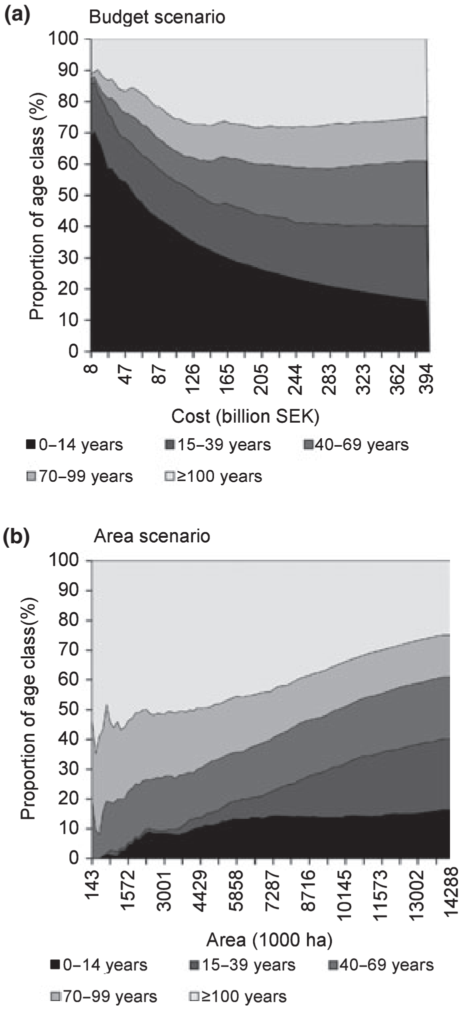

Fig. 2. Optimal age distributions of forest reserves in boreal Sweden plotted as a function of (a) cost and (b) area. The age distributions toward the left in the graphs are most relevant for the actual situation in Sweden, with about 6 billion SEK allocated to forest protection during the last 10-year period (Swedish Government. 2009), and with an environmental target of protecting an additional 900 000 ha. When the limits increase and approach the total area or total cost (the right hand side of the graphs) the age distribution equals the original distribution in the data set.

of 41 billion SEK, and was strikingly different with strong representation in the south-eastern part of the boreal region (Fig. 4b). As in the analysis on optimal age-distributions, the forests chosen in the budget-constrained scenario were mostly young, whereas the forests chosen in the area-constrained scenario were mostly old (Table 4).

The biodiversity indicator score in the scenarios with a budget constraint and an area constraint were both based on contributions from all indicators (Table 5). Indicators on dead wood were more represented in the budget-constrained scenario whereas large trees were much more represented in the area-constrained scenario. The goal programming approach led to a biodiversity indicator score in which the contributions of all indicators were higher, in some cases substantially, than the mean of their contribution when each indicator was maximized separately (Table 5).

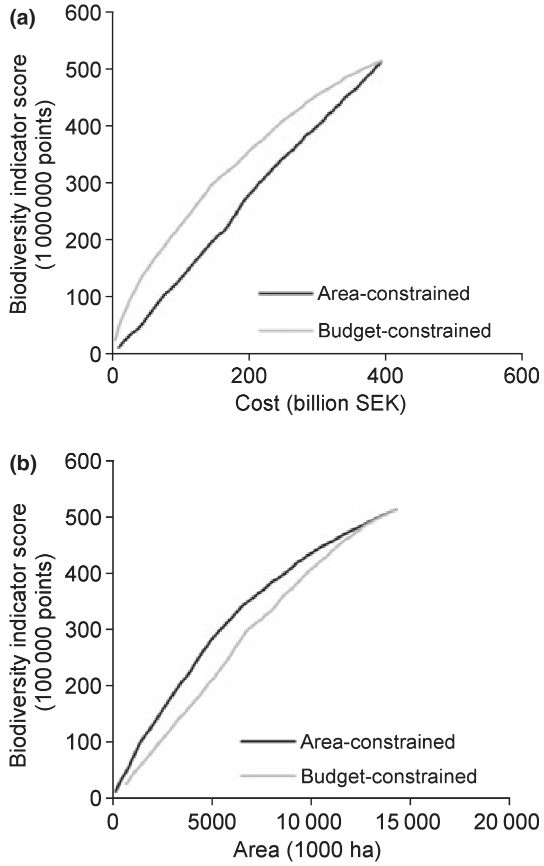

Fig. 3. The biodiversity indicator score plotted as a function of (a) cost and (b) area for the budget-constrained and area-constrained model.

Discussion

The results clearly show that it is more cost-effective to protect young forests and more area-effective to protect old forests, but that a combination of age classes always gives the highest biodiversity indicator score. This indicates that all age classes have a value to biodiversity, and that a reserve network ideally should consist of forests of different ages regardless of whether the selection is limited by budget or by area. This is also challenging since it demonstrates that there is a need to reorient current boreal forest conservation strategies, which almost exclusively target the oldest forests.

It was evident that it is more cost-effective to use a budget-constrained model compared to an area-constrained model when selecting reserves. Previous studies have shown that when land prices vary and area is used as a limitation, more money than necessary is spent, which is unfortunate since conservation is always restricted by scarce resources (Ando *et al.* 1998; Polasky, Camm & Garber-Yonts 2001). When using an area-constrained model the same biodiversity indicator score can be obtained in a smaller total area. Decision makers, therefore, have to integrate ecological and economic data and balance short- and long-term constraints in terms of cost and area in order to design cost-effective conservation strategies (Polasky, Camm & Garber-Yonts 2001; Juutinen *et al.* 2004; Messer 2006; Naidoo *et al.* 2006).

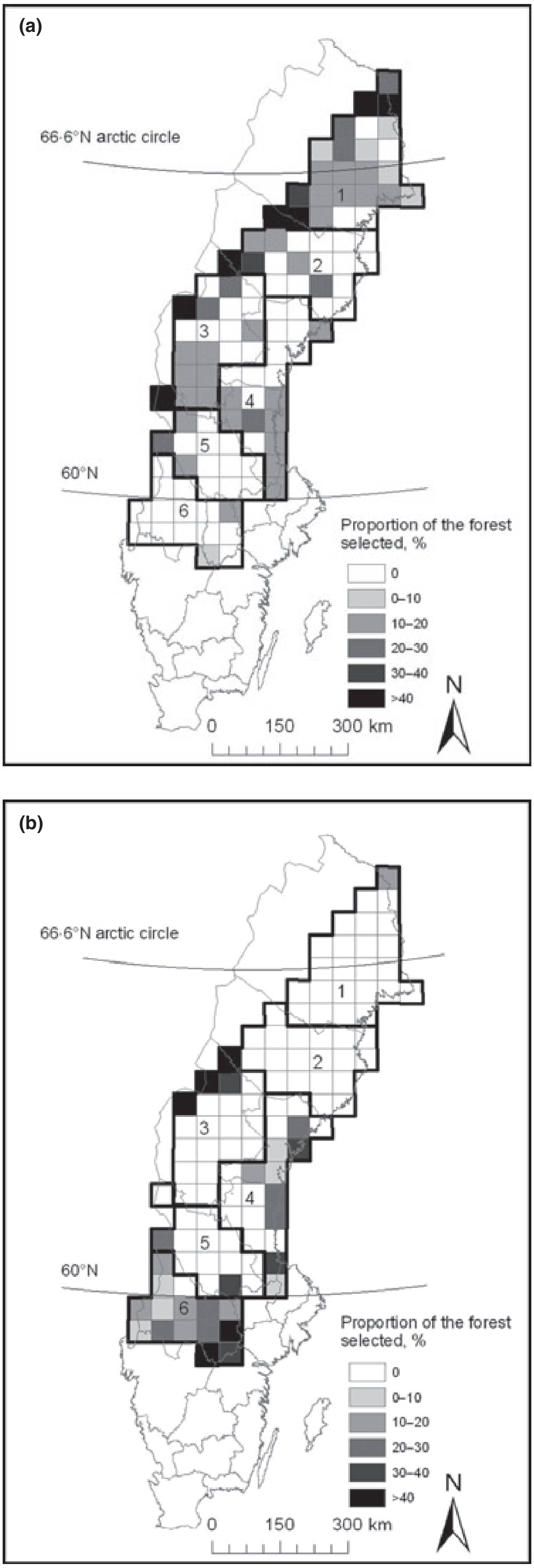

Fig. 4. The proportion of the total area selected in each 50 × 50 km plot with (a) a budget limit of 10 billion SEK (~9% of total area) or (b) an area limit of 715, 000 ha (~5% of total area). The biodiversity indicator score in both scenarios was approximately the same (51 million in the budget-constrained scenario and 50 million in the area-constrained scenario). For names of geographical regions see Fig. 1.

The analyses show that if costs are considered, large areas of young forests in north-western Sweden are selected. There are already numerous large nature reserves in this section of the boreal region, and more than 75% of all protected forests in the country are found here. However, the present reserves are overwhelmingly old, and by setting aside young, structurally rich forests nearby, dispersal and colonization of some species might be facilitated. One risk of concentrating reserves in the northwest region is that rare species confined to more eastern regions would not be protected

When costs are not considered, as in the area-constrained model, old forests are mostly selected and these are primarily located in the south-eastern section of the study area. One reason for this southern dominance could be a higher productivity, leading to higher representation of large trees, tentatively a subject to be further scrutinized in subsequent studies along with complementarity analyses between our model selections and existing reserves.

The NFI data showed that a majority of the structure-based variables of importance to biodiversity are most common in the oldest age classes, but that there are substantial amounts also found in younger forests. For the youngest age class, 0–14 years, this mainly reflects the practice of tree retention, (leaving trees for biodiversity at clear cutting) introduced in Sweden and other countries a few decades ago. However, at least in terms of dead wood the same pattern is also found following natural disturbances such as forest fires or storms, with plenty of dead wood present in the early successional stages, whilst amounts are lower at intermediate ages and then higher again in old-growth stages (Siitonen 2001). Much of the high conservation values of young forests reported here are thus likely to prevail both in young forests originating from management practices and in those originating from natural disturbances, although the latter would probably host higher amounts of dead wood and large living trees (Uotila *et al.* 2001).

The biodiversity indicators chosen were to some extent biassed towards features most common in old-growth forests (e.g. uneven age, multi-layered canopy and presence of large trees). A more unbiassed list of indicators would also include those that are important for rare species that prefer young age classes, such as sun-exposed dead trees (Kaila, Martikainen & Punttila 1997; Jonsell, Weslien & Ehnström 1998). Including a larger proportion of such indicators would further strengthen the result that young forests host important biodiversity potential.

There are some weaknesses in the structure-based approach. The same structures can be present in young and old forests, but support different species compositions, mainly due to

Table 4. Area distribution (proportion of selected area, %) in the six geographical regions and five age classes selected under a budget constraint of 10 billion SEK (~9% of the total area) and an area constraint of 714 000 ha (~5% of the total area)

	0–14 years	15–39 years	40–69 years	70–99 years	≥ 100 years	All age classes
Budget constraint 10 billion SEK (area 1·2 million ha)						
Norrbotten	22·6	9·8	0	1·2	5·6	39·2
Västerbotten	10·4	3·7	0·8	0	2·4	17·2
Jämtland	14·8	1·2	0·2	0·5	1·8	18·4
Västernorrland and Gävleborg	14·6	0	0	0	0	14·6
Dalarna	6·3	1·2	0·8	0	0	8·3
Värmland and Örebro	2·3	0	0	0	0	2·3
All regions	70·8	15·8	1·8	1·8	9·8	100
Area constraint 714 000 ha (cost 41 billion SEK)						
Norrbotten	0	0	0	0	0·6	0·6
Västerbotten	0	0	0	0	4·2	4·2
Jämtland	0	0	0·3	0·7	10·6	11·6
Västernorrland and Gävleborg	1·5	0	0	15·8	9·0	26·2
Dalarna	0	0	0	3·2	7·8	11·0
Värmland and Örebro	0	0	16·7	13·4	16·3	46·4
All regions	1·5	0	17·0	33·0	48·5	100

Table 5. The contribution to the biodiversity indicator score of each indicator from both phases in the goal programming under a budget constraint and an area constraint

	Budget scenario				Area scenario			
Biodiversity indicator	Max[1]	Mean[2]	Min[3]	% of mean[4]	Max	Mean	Min	% of mean
Uneven age	56986	26488	15502	145	79266	52006	25247	112
Gaps	48442	24171	8801	143	43714	24332	18587	110
Stand character	7306	1265	0	131	9832	2122	100	133
Tree layer	59801	32115	14258	182	58258	39889	28864	164
Ground structure	69991	32317	9415	211	61775	35602	21916	201
Large pine	14910	6005	2559	109	38861	16751	8570	120
Large spruce	9682	2258	139	138	30494	13372	4019	115
Large birch	2944	542	149	138	6176	1873	398	106
Large aspen	1953	313	36	176	3780	860	150	224
Large deciduous tree	1574	234	49	166	2498	510	149	202
Dead conifer tree lying	32103	14262	4814	149	24202	11366	4995	179
Dead deciduous tree lying	11012	3907	1199	123	10475	3240	1804	141
Dead conifer tree standing	12124	4746	2351	140	19116	8924	4108	173
Dead deciduous standing	5090	1150	199	127	7990	2429	700	103
Presence of rowan	62552	27191	7429	261	57944	24975	10306	179
Affected by water	5789	1106	301	125	8756	1934	700	111
Volume of dead wood[5]	66677	33714	13509	150	70850	39003	18945	127

[1]The biodiversity indicator score when maximizing each indicator separately (the goal) gives a maximal sum of points that each indicator can obtain (when the optimization is made only considering that specific indicator).
[2]A mean sum of points from all 17 goal optimizations.
[3]The lowest sum of points that the indicator gets from another indicator's goal optimization.
[4]The minimization of all indicator's quadratic percentage deviation from their goal (phase 2 in the goal programming) gives a contribution from each indicator to the biodiversity indicator score shown here as the percentage of its mean value.
[5]Shown in units of 1000 points.

differences in microclimatic conditions and colonization opportunities. Further, the presence of structures is no guarantee of the presence of associated species since other aspects, such as forest history and connectivity might be decisive for species occurrences (Nilsson, Hedin & Niklasson 2001). Therefore, a further development of our study would be to repeat the analyses for species distribution data and compare the results with those based on structural data. There are detailed data on occurrences of red-listed species from organism groups such as vascular plants, birds, bryophytes, lichens and fungi in boreal Sweden which could be used for such a comparison.

The proposed goal programming approach provides impartial and objective weighting. We used the same weighting for analysis of the deviation from the goals, but this can be easily modified if desired. If weights are decided manually, care must be taken since the results can greatly disadvantage some

variables (Table 5, 'Min' column). We note that the importance of different indicators are indirectly weighted when deciding criteria for points, but those decisions are based on existing knowledge of which features are important for biodiversity. A further development of the model could potentially be to add specific requirements regarding geographical distribution or a minimum amount of different indicators. This, however, needs to be substantiated by high-quality ecological studies on the critical requirements of different species.

In northern Europe, with its long history of relatively intense forest use, there are so few old-growth forests left that areas strongly impacted by humans need to be included when new forests are protected. Consequently, it is vital to prioritize the few high-quality old-growth remnants that still exist, although our analyses indicate that it is more cost-effective to include young forests in reserve networks. The young forests that we propose for protection have a decidedly different character than those normally regenerating after clear-cutting, even with tree retention. A careful selection will be needed for sites especially rich in dead wood, remnant live trees and other qualities of importance to biodiversity. Protection of young forest allows much more land to be set aside than protection of old-growth forest, due to lower net present values. A shift towards more protection of young forest might therefore eventually cause a reduction in timber volumes available for forest industry. A novel conservation strategy, and a future research challenge, is to analyse if some reserves with old forests could be systematically replaced by younger forests without causing biodiversity decline at the landscape level. Possibly, such a dynamic reserve scheme could benefit both timber production and biodiversity protection. In general, early-successional stages are overlooked in forest conservation. Thus, our approach with protection of different age classes has a general interest also for other biomes where biodiversity is adapted to frequent disturbances and where early successional stages are common in natural forest landscapes.

Acknowledgements

We thank Per Nilsson for help with the NFI-data and Peder Wikström and Torgny Lind for assistance during the Heureka calculations. We also thank Viktor Johansson and three anonymous reviewers for constructive comments on the manuscript. The study was financially supported by FORMAS.

References

Ahti, T., Hämet-Ahti, L. & Jalas, J. (1968) Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici*, **5**, 169–211.

Ando, A., Camm, J., Polasky, S. & Solow, A. (1998) Species distributions, land values, and efficient conservation. *Science*, **279**, 2126–2128.

Angelstam, P. (1998) Maintaining and restoring biodiversity in European boreal forests by developing natural disturbance regimes. *Journal of Vegetation Science*, **9**, 593–602.

Anonymous. (1932) *Uppskattning av Sveriges skogstillgångar*. Jordbruksdepartementet, Stockholm, Sweden (in Swedish).

Anonymous. (2005) *RIS Riksinventeringen av skog. Fältinstruktion 2005*. Institutionen för skoglig resurshushållning och geomatik SLU, Umeå, Sweden (in Swedish).

Anonymous. (2007a) *Skogsstatistisk årsbok 2007*. Sveriges officiella statistik, Skogsstyrelsen, Jönköping, Sweden (in Swedish).

Anonymous. (2007b) *Skogsdata 2007*. *Sveriges officiella statistik*, Institutionen för skoglig resurshushållning, SLU, Umeå (in Swedish).

Esseen, P.A., Ehnström, B., Ericson, L. & Sjöberg, K. (1997) Boreal forests. *Ecological Bulletins*, **46**, 16–47.

FAO (Food and Agriculture Organization of the United Nations). (2006) *Global Forest Resources Assessment 2005: Progress towards sustainable forest management*. FAO, Rome, Italy.

Ferris, R. & Humphrey, J.W. (1999) A review of potential biodiversity indicators for application in British forests. *Forestry*, **72**, 313–328.

Gärdenfors, U. (Ed.). (2005) *The 2005 Red List of Swedish Species*. Swedish Species Information Centre, Swedish University of Agricultural Sciences, Uppsala, Sweden.

Gustafsson, L. & Ahlén, I. (1996) *The National Atlas of Sweden. Geography of Plants and Animals*. SNA, Stockholm, Sweden.

Hagar, J.C. (2007) Wildlife species associated with non-coniferous vegetation in Pacific Northwest conifer forests: a review. *Forest Ecology and Management*, **246**, 108–122.

Ibbotson, R.G. & Sinquefield, R.A. (1986) *Stocks, Bonds, Bills and Inflation: 1986 Yearbook*. Ibbotson Associates, Chicago.

ILOG (2008) *CPLEX* system 11.2. Gentilly, France.

Jonsell, M., Weslien, J. & Ehnström, B. (1998) Substrate requirements of red-listed saproxylic invertebrates in Sweden. *Biodiversity and Conservation*, **7**, 749–764.

Junninen, K., Simila, M., Kouki, J. & Kotiranta, H. (2006) Assemblages of wood-inhabiting fungi along the gradients of succession and naturalness in boreal pine-dominated forests in Fennoscandia. *Ecography*, **29**, 75–83.

Juutinen, A., Mantymaa, E., Mönkkönen, M. & Salmi, J. (2004) A cost-efficient approach to selecting forest stands for conserving species: a case study from northern Fennoscandia. *Forest Science*, **50**, 527–539.

Kaila, L., Martikainen, P. & Punttila, P. (1997) Dead trees left in clear-cuts benefit saproxylic Coleoptera adapted to natural disturbances in boreal forest. *Biodiversity and Conservation*, **6**, 1–18.

Kouki, J., Löfman, S., Martikainen, P., Rouvinen, S. & Uotila, A. (2001) Forest fragmentation in Fennoscandia: linking habitat requirements of wood-associated threatened species to landscape and habitat changes. *Scandinavian Journal of Forest Research*, **16**, 27–37.

Kuuluvainen, T. (2002) Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica*, **36**, 97–125.

Kuuluvainen, T. (2009) Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. *AMBIO: A Journal of the Human Environment*, **38**, 309–315.

Lämås, T., Dahlin, B., Olsson, H., Sallnäs, O., Stenlid, J. & Ståhl, G. (2006) Preface. *Scandinavian Journal of Forest Research*, **21**, 3–4.

Lindenmayer, D.B. & Franklin, J.F. (2003) *Towards Forest Sustainability*. CSIRO Publishing, Melbourne, Australia.

Lindenmayer, D.B., Margules, C.R. & Botkin, D.B. (2000) Indicators of biodiversity for ecologically sustainable forest management. *Conservation Biology*, **14**, 941–950.

Löfman, S. & Kouki, J. (2001) Fifty years of landscape transformation in managed forests of Southern Finland. *Scandinavian Journal of Forest Research*, **16**, 44–53.

Lundgren, J., Rönnqvist, M. & Värbrand, P. (2010) *Optimization*. Studentlitteratur, Lund, Sweden.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Messer, K.D. (2006) The conservation benefits of cost-effective land acquisition: a case study in Maryland. *Journal of Environmental Management*, **79**, 305–315.

Naidoo, R., Balmford, A., Ferraro, P.J., Polasky, S., Ricketts, T.H. & Rouget, M. (2006) Integrating economic costs into conservation planning. *Trends in Ecology & Evolution*, **21**, 681–687.

Nilsson, S.G., Hedin, J. & Niklasson, M. (2001) Biodiversity and its assessment in boreal and nemoral forests. *Scandinavian Journal of Forest Research*, **16**, 10–26.

Östlund, L., Zackrisson, O. & Axelsson, A.L. (1997) The history and transformation of a Scandinavian boreal forest landscape since the 19th century. *Canadian Journal of Forest Research*, **27**, 1198–1206.

Polasky, S., Camm, J.D. & Garber-Yonts, B. (2001) Selecting biological reserves cost-effectively: an application to terrestrial vertebrate conservation in Oregon. *Land Economics*, **77**, 68–78.

Ranneby, B., Cruse, T., Hägglund, B., Jonasson, H. & Swärd, J. (1987) *Designing a New National Forest Survey for Sweden*. Swedish University of Agricultural Sciences, Uppsala, Sweden.

Siitonen, J. (2001) Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. *Ecological Bulletins*, **49**, 11–41.

Spanos, K. & Feest, A. (2007) A review of the assessment of biodiversity in forest ecosystems. *Management of Environmental Quality: An International Journal*, **18**, 475–486.

Spies, T.A. & Franklin, J.F. (1991) *The Structure of Natural Young, Mature, and Old-growth Douglas-fir Forests in Oregon and Washington*. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR, USA.

Swanson, M.E., Franklin, J.F., Beschta, R.L., Crisafulli, C.M., DellaSala, D.A., Hutto, R.L., Lindenmayer, D.B. & Swanson, F.J. (2010) The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, in press. doi: 10.1890/090157.

Swedish Government. (2005) *Svenska miljömål – ett gemensamt uppdrag*. *Proposition 2004/2005:150*. Swedish Government, Stockholm, Sweden (in Swedish).

Swedish Government. (2009) *Hållbart skydd av naturområden*. *Proposition 2008/09:214*. Swedish Government, Stockholm, Sweden (in Swedish).

Tikkanen, O., Martikainen, P., Hyvarinen, E., Junninen, K. & Kouki, J. (2006) Red-listed boreal forest species of Finland: associations with forest structure, tree species, and decaying wood. *Annales Zoologici Fennici*, **43**, 373–383.

Uotila, A., Maltamo, M., Uuttera, J. & Isomäki, A. (2001) Stand structure in semi-natural and managed forests in eastern Finland and Russian Karelia. *Ecological Bulletins*, **49**, 149–158.

Zackrisson, O. (1977) Influence of forest fires on the North Swedish boreal forest. *Oikos*, **29**, 22–32.

Received 9 March 2010; accepted 20 October 2010
Handling Editor: Harald Bugman